

The pollination specialization of *Habenaria decaryana* H. Perr. (*Orchidaceae*) in Madagascar

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Summary : Studies of *Habenaria decaryana* H. Perr. (*Orchidaceae*) in a primary forest on the Ankazobe tampoketsa, Central Madagascar, showed that the plant is phalaenophilous. The pollinaria attach to the ventral inner surface of the eyes of noctuid and perhaps also geometrid moths. Pollination is effected by moths after the pollinia have undergone a hygroscopic downward movement, which presents them in the correct position relative to the stigmatic lobes : a mechanism which promotes xenogamy.

Résumé : L'étude d'*Habenaria decaryana* H. Perr. (*Orchidaceae*) dans une forêt primaire du tampoketsa d'Ankazobe, Madagascar Centre, indique que la plante est phalénophile. Les pollinaires adhèrent à la surface ventrale interne des yeux des lépidoptères noctuidés et peut-être aussi géométridés. La pollinisation est effectuée par ces insectes après que les pollinies aient subi un mouvement hygroscopique de haut en bas les présentant dans une position adéquate par rapport aux lobes stigmatiques, mécanisme favorisant la xénogamie.

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The orchid genus *Habenaria* Willd. contains around 800 terrestrial species and is present below 4,000 m throughout the tropics (RENZ, 1980). There is little information on the pollination specializations in *Habenaria*. Floral features suggest that the sphingophilous and phalaenophilous syndromes predominate (cf. DRESSLER, 1981). The only record of a pollinating insect is from South Africa ; the hawk-moth *Hippotion celerio* (L.) is reported to have visited the flowers of *Habenaria epipactidea* Rchb. f. (*H. polyphylla* Kraenzl.) (VOGEL, 1954). During nectar-drinking the hawk-moth supported itself by the front legs on the flowers and thereby touched against the viscidia on the two rostellar projections. The pollinaria attached to the front tarsi, from which pollen could be transferred to the stigmatic projections of flowers visited later. VOGEL (1954) suggested for *H. falcicornis* (Lindl.) H. Bolus var. *caffra* (Schltr.) Renz & Schelpe (*H. tetrapetala* Kraenzl.) that the extremely extended rostellar projections interact in sternotribic pollination by hawk-moths.

Habenaria decaryana H. Perr. is a robust, about one meter high Malagasy endemic. It occurs in moist habitats along watercourses in the remaining patches of primary forest on the Central Plateau of Madagascar. During the period 13-30 November 1983 we had the opportunity to study the pollination specialization of this plant in the Ambohitantely forest, 25 km NW of Ankazobe on the Ankazobe tampoketsa.

OBSERVATIONS

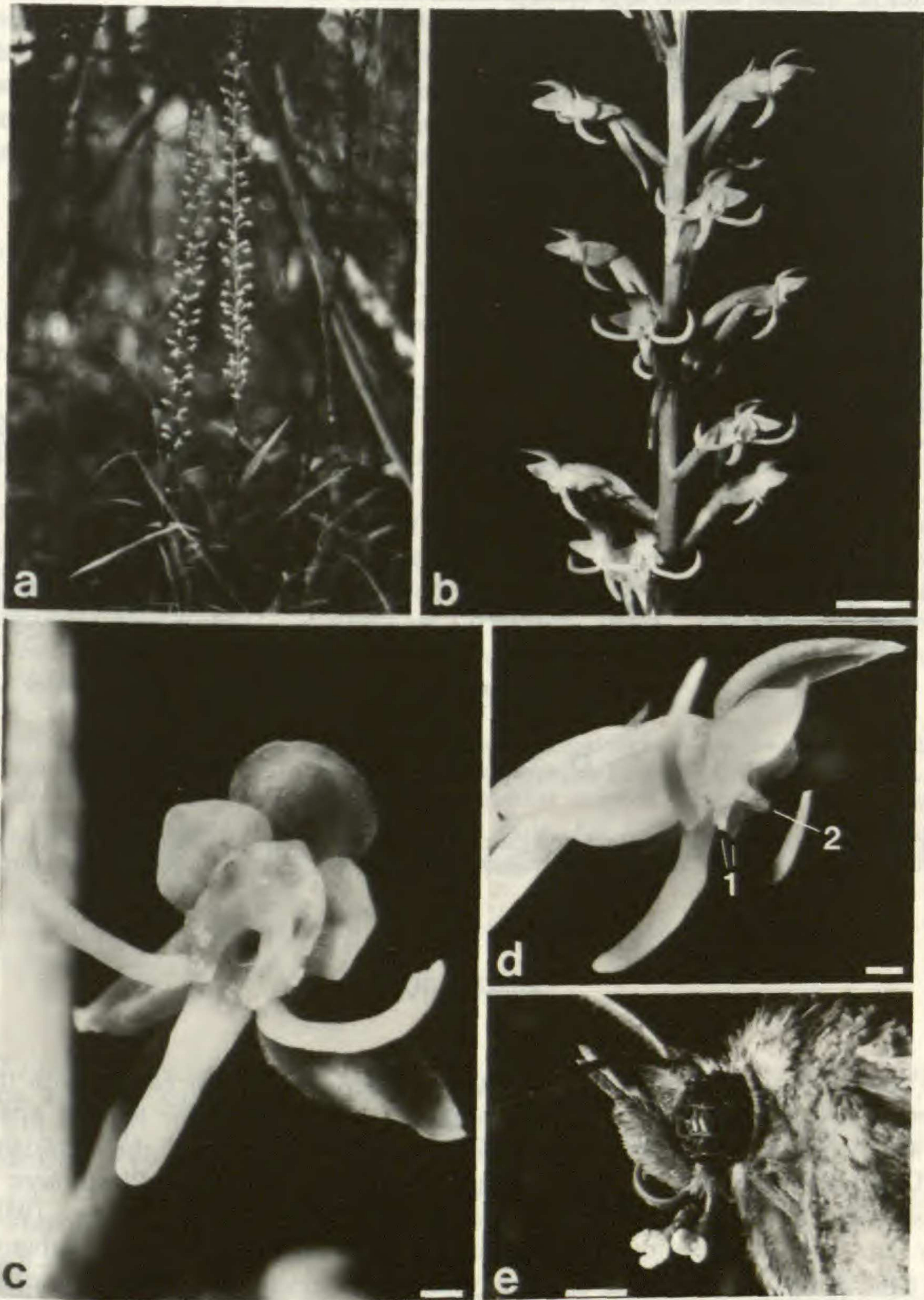
Floral morphology

The 40-60 cm long, lax inflorescence bears 50-100 greenish white flowers which are 11-15 mm across (Pl. 1, *a*). The flower-lip is profoundly tripartite. Its central lobe curves evenly backwards while the filamentous lateral extend basally, and form two upcurved "arms" (Pl. 1, *b-d*). The 13-20 mm long spur is subparallel with the ovary, distinctly dilated at about the middle, and filled with nectar to approximately one third of its length (Pl. 1, *b*). The rostellar projections are relatively short (Pl. 1, *d*), only about 0.6 mm, and support two moderately long-caudicled pollinia (Pl. 2, *a*). The caudicles of the pollinia are ca. 1.2 mm long. The viscidia are positioned at the apices of the rostellar projections and are small (about 0.3 mm in diameter), and lack differentiated discs (Pl. 2, *b*). The distance between the viscidia is ca. 1.3 mm. Each viscidium membrane contains a hygroscopic sticky mass of cells which has the capacity both to attach the pollinarium onto an object that has ruptured the membrane, and to rotate the pollinium downwards as the viscidia desiccate into a firm brownish structure when withdrawn from the flower. The stigma extends along both sides of the spur-mouth, with its two lobes protruding ventrally (Pl. 1, *c, d*). The flowers emit a distinct sweet scent after dusk.

Pollination

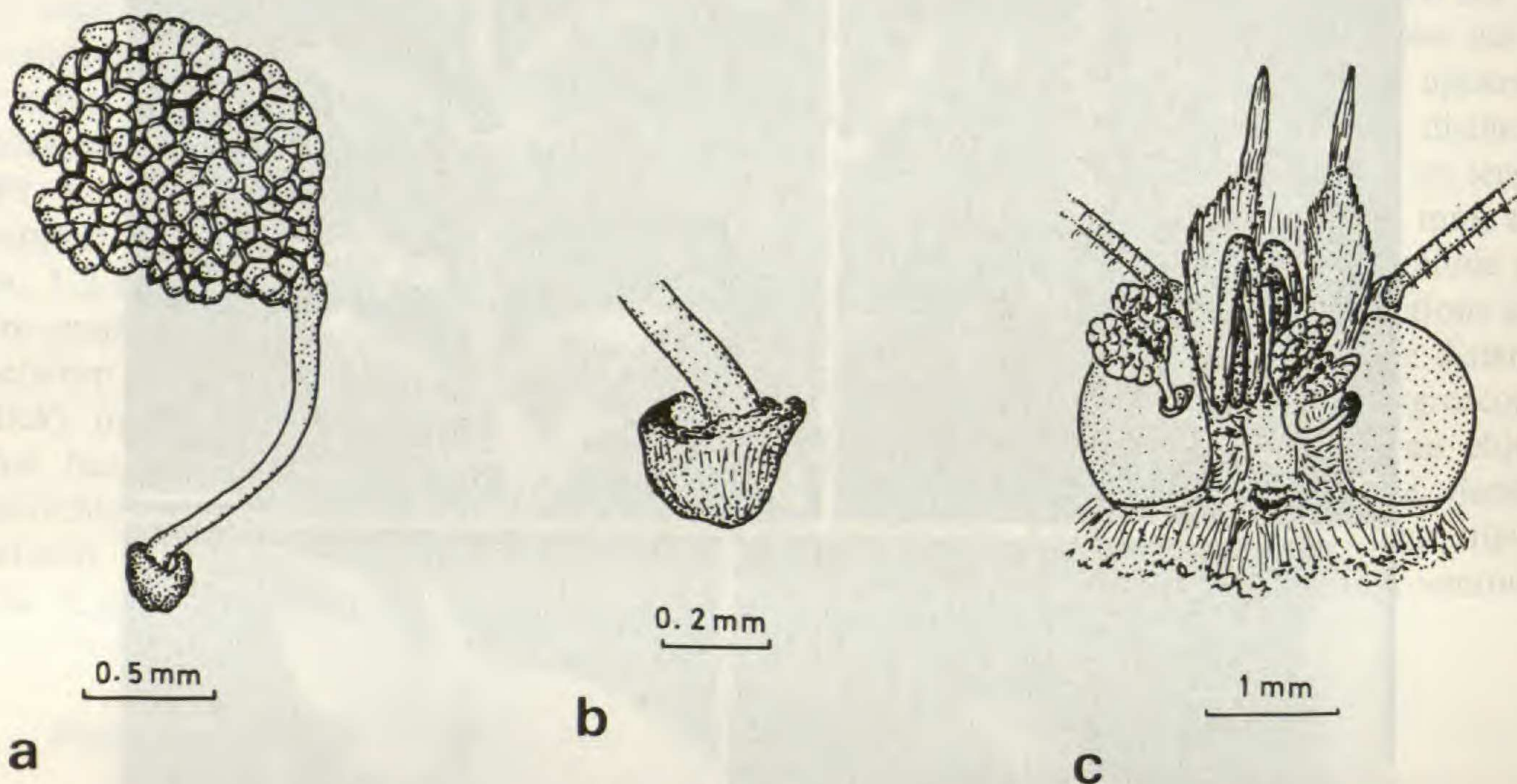
No flower-visitors were observed on *H. decaryana* but we succeeded in capturing a pollen vector, *Remigiodes remigina* (Mab.) ♂ (*Noctuidae, Catocalinae*) by means of a light-trap placed at the border of the forest about 30 m from the nearest flowering individual. The pollinaria were transported on the eyes of the moth (Pl. 1, *e*). The viscidia were affixed to the ventral surface close to the eye-margins and at a distance of 1.3 mm from each other (Pl. 2, *c*). The width of the head across the eyes and the distance between the ventral eye-margins in *R. remigina* were 3.1 and 1.0 mm, respectively. The length of the proboscis was 12.0 mm, thus distinctly shorter than the spur-length of the orchid.

Comparison between the floral morphology of *H. decaryana* and the pollen vector *R. remigina* suggests the following mechanism for the removal of pollinaria and subsequent pollination. The moths alight and insert their probosces while sitting head-up on the flowers. They presumably gain support by the lateral "arms" of the labellum. In draining the nectar, the moths are stimulated to force the entire length of their probosces into the spur due to the spur with the distally-located nectar being longer than the probosces. As the moths press their heads against the column the surface membrane of the viscidia ruptures. Viscid matter cements the pollinaria onto the touching surface of the moths which, due to the position of the viscidia on the column in relation to the moths' heads, will normally be the ventral inner surface of the eyes. When the moths withdraw, the pollinia are extracted from the anther pockets and, at this stage, project forwards from the



Pl. 1. — *Habenaria decaryana* in Ambohitantely forest, Central Madagascar : a, flowering stalks ; old infructescence to the right ; b, part of inflorescence ; scale : 1 cm ; c, flower in front view ; scale : 1 mm ; d, flower in lateral view (1, stigmatic projections ; 2, rostellar projections) ; scale : 1 mm ; e, the moth *Remigiodes remigina* (Mab.) ♂ (*Noctuidae, Catocalinae*) with one pollinarium attached to each eye ; scale : 1 mm.

eyes. After a minute or so, hygroscopic action rotates the pollinia so that they point downwards (cf. Pl. 1, e) into a position in which they will strike the stigma lobes in the flowers that are subsequently visited by the moths. Naturally pollinated stigmas that were examined had large numbers of massulae deposited distally on the ventrally projecting lobes. However, several incompletely extracted pollinaria with viscidia exhibiting numerous scales and hairs detached from the heads of visiting moths were also observed, suggesting that the floral mechanism sometimes fails.



Pl. 2. — Pollinaria of *Habenaria decaryana* and their attachment on moths : a, pollinarium ; b, viscidium and part of caudicle ; c, head of *Remigiodes remigina* ♂ with two pollinaria attached ; strictly ventral view.

DISCUSSION

The pollination specialization in *H. decaryana* reconciles rather closely with that found in species of *Platanthera* L. C. Rich. which exhibit viscidia more or less far apart on the column and which affix their pollinaria onto the eyes of moths, e.g. the Eurasian *P. chlorantha* (Cust.) Rchb. (DARWIN, 1862 ; NILSSON, 1978). In the genus *Platanthera* such specialization seems to exist in about half the number of species (vide NILSSON, 1981). Most probably the "eye-specialization" is also frequent in *Habenaria* since the number of species is great and sphingophily and phalaenophily certainly prevail. This prediction is strongly supported by the fact that moths are singularly hairy and scaly insects with few alternative surfaces for efficient attachment of viscidia (cf. NILSSON, 1983).

The great diversity of the rostellar and stigmatic projections that occur in *Habenaria* (cf. WILLIAMSON, 1977 ; STEWART et al., 1982) reflects most probably adaptations which maximize components in male and female fitness, i.e. (in the male) : deposition of pollina-

ria on the vector and of pollen on conspecific stigmas, and (in the female) capture of mas-sulae by the stigma. In many species these projections are long, suggesting that several ventral structures on moths are exploited for pollen transport (cf. VOGEL, 1954). In *H. decaryana* the pollinaria are also deposited ventrally on the vector. In contrast, ventral pollination by moths is not known to occur in the genus *Platanthera*, except via the proboscis (INOUE, 1983).

The length relationship between the spur in *H. decaryana* and the shorter proboscis of a pollen vector such as *R. remigina* promotes efficient contact between visitor and floral sexual organs. Similar morphological relationships are also involved in other orchids, for example *Platanthera* spp. (NILSSON, 1978, 1983 ; INOUE, 1983), and also long-spurred angraecoid orchids such as *Angraecum arachnites* Schltr. which grows in the same forest as *H. decaryana* (NILSSON et al., 1985), and *A. sesquipedale* Thou. (NILSSON et al., unpubl.). The "long spur — short proboscis" specialization seems to be a widely adopted principle in moth — orchid relationships and probably has a simple evolutionary explanation : plant individuals with shorter spurs than the proboscis of visiting moths are at a selective disadvantage since their columns suffer from reduced visitor contact (cf. NILSSON, 1983). At the same time the evolution of spur-length may be associated with the evolution of proboscis length of moths in a process of diffuse coevolution (*sensu* JANZEN, 1980). Many African and Malagasy species of *Habenaria* have very long spurs indicative of sphingophily (cf. WILLIAMSON, 1977 ; PERRIER DE LA BÂTHIE, 1939). The relatively short spur in *H. decaryana* reflects that this plant is phalaenophilous and not sphingophilous, subject to stabilizing selection by noctuid and perhaps geometrid moths.

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